SHORT COMMUNICATION

What is the function of 'pre-dispersal' behavior in juvenile social spiders (*Stegodyphus dumicola*: Eresidae)?

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Abstract. Bridging and ballooning dispersal in spiders are preceded by "tiptoe" behavior, in which the spider stands on the tips of its eight tarsi, with the legs extended downward and the abdomen raised, and releases one or more silk lines. The occurrence of tiptoe behavior has been used in experiments to indicate a propensity to initiate dispersal. Juvenile social spiders *Stegodyphus dumicola* Pocock 1898 (Eresidae) exhibited tiptoe behavior while walking along the upper strands of the capture web at night. Simultaneously, they released long silk lines that streamed upward. These behaviors were not followed by dispersal. In wind-tunnel tests we found that tiptoe behavior increased with time during the evening activity period and occurred with higher frequency in small individuals. We suggest that tiptoe behavior in juveniles of *S. dumicola* is not associated with dispersal, but is more likely a component of web-building.

Keywords: Ballooning, bridging, tiptoe behavior, web-building, wind tunnel

Many spiders use ballooning for long-distance dispersal (Foelix 2011). Aerial dispersal is particularly common in araneomorphs, and occurs more often in juveniles than in adults, although in small species such as many linyphiids, adults disperse in this manner. Aerial dispersal is typically initiated by "tiptoeing": the spider stands on the tips of its eight tarsi, with the legs extended and the abdomen raised, and releases one or more silk lines. The immediate function of tiptoe behavior is to elevate the spider's spinnerets, thereby increasing the velocity of air flowing past them and facilitating the release of silk (Suter 1999; Foelix 2011). When enough upward force is generated on the silk, the spider releases its grip on the substrate and becomes airborne (Suter 1991, 1999). Aerial dispersal can also be initiated when the spider descends on a dragline and releases a free-ended line and is eventually carried off on the line (Eberhard 1987).

Tiptoe behavior also occurs in the context of bridging or rappelling, a form of short-range dispersal (Eberhard 1987), in which the end of the released line becomes snagged on an object and the spider then uses the line as a bridge. Numerous experimental studies of dispersal conducted in wind tunnels have used tiptoe behavior as an indication of the propensity to initiate ballooning or bridging dispersal, and have referred to it as "pre-dispersal behavior" (e.g., Weyman et al. 2002; Weyman 1995; Bonte et al. 2003; Bonte et al. 2009; Larrivée & Buddle 2011).

The release of free-ended lines, however, is not restricted to dispersal: it may occur in the initial stages of web construction as well. The first stage of web building involves establishment of a bridge thread between two separated points (Foelix 2011). Bridging behavior during web construction may be initiated when the spider releases a silk line, which drifts with the air current, becomes snagged and is then reinforced. Release of the bridging line was described as similar to "spontaneous" initiation of lines (Eberhard 1987), when the spider stood with its abdomen lifted and silk was drawn out in the breeze (S. Zschokke personal communication). Thus, tiptoe behavior may be a reasonable indicator of dispersal in species that do not build webs, but is perhaps not an unambiguous indicator in web-building species.

During observations of colonies of the social spider, *Stegodyphus dumicola* Pocock 1898 (Eresidae) in Namibia, we saw juveniles adopting the tiptoe stance on upper strands of the capture web during the start of their activity period at dusk. Under the assumption that tiptoe behavior indicates dispersal propensity, we expected to see these spiders lift off the web or rappel to nearby vegetation. Instead, the spiders moved along the web and alternated between laying down dragline silk on the web and adopting tiptoe behavior. This observation led us to question the function of tiptoe behavior in juvenile *S. dumicola*. To obtain insight into the contexts in which this behavior occurs and its possible function, we observed juveniles on the web, and we collected individuals from webs during their activity period and tested their behavior in a wind tunnel.

We investigated colonies of *S. dumicola* at Uisib farm (19°33'S, 17°13'E), near Otavi, in northern Namibia during January 2011 (southern hemisphere summer). A colony consists of a nest of dense silk and leaves, and one or more loosely constructed, cribellate-silk sheet webs radiating out of the nest in different planes. A nest may contain a few to several hundred individuals (Seibt and Wickler 1988). Colonies increase in size by inbreeding within the nest and by retention of juveniles in the colony (Lubin & Bilde 2007).

Eleven colonies were located in grassy roadside vegetation. Nests were attached to shrubs or small trees at a height of 0.2–1.5 m and contained mostly juveniles and a few subadult and adult males. We observed spiders in two medium-sized colonies on shrubs separated by 6 m (nest dimensions: 0.25–0.3 m length and ca. 0.2 m wide) and one large colony (nest ca. 0.5 m diameter) located in a tree about 100 m from the other two colonies. All nests had extensive capture webs that occasionally were damaged by heavy rains and livestock. We observed the behavior of 5–10 spiders per colony, chosen haphazardly, for up to 30 min per colony, between 17:00 and 22:00 local time (GMT+1), when spiders were active in web repair and prey capture. We observed the first two colonies during five nights between 11–20 January 2011, and the third colony on a single night. We did not quantify the observations and our notes serve only to describe the behaviors as we observed them in nature.

In testing for pre-dispersal behaviors, we adopted a technique similar to that used by other researchers (e.g., Weyman 1995). The wind tunnel had 0.3 × 0.6-m glass sides and a fan at one end. The fan drew air through the chamber at velocities that could be regulated both by adjusting fan speed and by opening or closing vents along the seal between the fan and the chamber. We did not attempt to reduce turbulence in the air flowing into the 0.3 × 0.3 m opening of the wind tunnel. In our tests, wind speed varied between 0.5 and 0.7 m/s, measured with a digital anemometer (Kestrel 4000, KestrelMeters.com).

The wind tunnel was suspended above a table at a ~45° angle with the surface of the table. On the table, at the lower end of the wind tunnel, we placed a bowl filled with water, with a 0.3 m long wooden dowel fixed at a 45° angle in a plasticine base in the center of the bowl, protruding into the wind tunnel. Some silk from the nest being tested was wrapped around the upper part of the dowel. The water prevented the escape of the spider.

We collected juvenile spiders (total body length, mean ± SD = 7.3 ± 0.9 mm, range: 4.6–9.2 mm, n = 79) for the experiments 0.5–2 h before testing (during 18:30–21:50) from the three colonies noted above. The juveniles were likely to be females, as subadult and adult males were already present in all three colonies; males mature before females, and the colony sex ratio is highly female biased (Henschel et al. 1995). We used soft forceps or a vial to collect groups of juveniles active in web-building or groups of juveniles on prey. We kept the spiders in these groups, classified according to source nest and activity on the web. Each spider was released onto the dowel individually, and we observed the behavior in the wind tunnel for up to 5 min using weak headlamp lighting. Each spider was tested only once. We segregated the spiders into two groups after testing according to whether or not they exhibited tiptoe behavior within 5 min of being placed on the dowel and measured them with calipers (total body length and prosoma width, measured with digital calipers to 0.1 mm). We conducted the tests during January 11–20, 2011, between 19:30–22:40. Air temperature during the tests was 20.5–25.2° C, and late afternoon rains ensured high humidity.

We documented tiptoe behavior using a DSLR camera (Nikon D200) fitted with a 105-mm macro lens and two off-camera flashes, one to illuminate the spider and the other providing strong backlighting to make the spider's silk visible. Spider-to-lens distance was approximately 0.2 m.

Analyses were done in Statistica v9 (StatSoft, Inc.), and data were log (x+1) transformed where necessary to normalize residuals.

Spider observations.—At dusk (19:00–19:30 local time) juveniles emerged from the nest and walked on the web with draglines. Some walked on the thicker frame threads at the edges of the colony web, then stopped and performed tiptoe behavior, releasing very fine silk lines that were visible only in favorable lighting. There appeared to be more than a single line released by an individual. Some juveniles walked with raised abdomen while continuing to release lines. Tiptoe durations were ≤ 30 s and individuals repeatedly alternated between tiptoe behavior, dragline laying and attaching silk to the web. We never observed transitions between spinning cribellate silk and tiptoe behavior. Using strong backlighting, we could see meters-long thin lines streaming upward from the thick frame silk where no spiders were present, suggesting that the spiders had attached the proximal ends of the lines to the web. The movement of these lines indicated that the distal ends remained free.

Wind-tunnel tests.—Juvenile S. dumicola released onto the dowel exhibited several behaviors (Table 1): questing; walking; dropping on a dragline, sometimes with release of a thinner, free-ended line; and tiptoeing. The dragline originated from the anterior spinnerets, while the free-ended thin lines, released when tiptoeing (Fig. 1) or when hanging from a dragline, originated from the posterior spinnerets. In some instances, it appeared that more than one line was released from each of the posterior spinnerets.

Overall, 53.2% of juveniles (n = 77) exhibited tiptoe behavior; 14 dropped on a dragline, nine of which also tiptoed. We could not ascertain whether spiders dropping on a dragline always released additional free-ended lines. There was no significant difference in the frequency of tiptoeing in the three nests (χ^2 = 4.435, df = 2, P > 0.1); therefore, in the following analyses data from the three nests were combined.

The first tiptoe behavior in the wind-tunnel tests occurred at 19:50 local time, 20 min after the first individual was tested and during the period when tiptoeing was observed on the webs. The probability of

Table 1.—Description of behaviors seen in spiders placed on the wooden dowel in the wind tunnel experiments.

Behavior	Description
Quest	Waves legs I in a rotating fashion, either when stationary or while walking with the remaining 6 legs.
Walk	Walks using all eight legs and laying a dragline.
Drop on dragline	Drops on dragline to the substrate, or drops a few cm and hangs on a dragline. When hanging the spider often lets out another line that is caught by the air current.
Tiptoe	Stands on the tips of the tarsi of all 4 pairs of legs, either on the side of the stick or at the top, and releases a silk line that is caught in the air current.

tiptoeing increased significantly with time during the night (logistic regression for binomially distributed data, Wald statistic, W = 10.69, P = 0.001, n = 76). This was also the case when we considered only those spiders engaged in web building when collected (W = 8.397, P = 0.004, n = 28, Fig. 2). Juveniles that were engaging in web repair when they were removed from the web exhibited a somewhat, but not significantly, higher frequency of tiptoe behavior (64.3%) than juveniles collected on prey (39.3%) (Pearson's χ^2 = 3.42, n = 56, df = 1, P = 0.065). Spiders that exhibited tiptoe behavior were significantly smaller in prosoma width than those that did not (Table 2).

Possible functions of tiptoe behavior in S. dumicola.—Social S. dumicola disperse to establish new nests by ballooning (long-distance dispersal) and by budding (colony fission) (Schneider et al. 2001; Bilde et al. 2007; Lubin et al. 2009). Adult females engage in aerial dispersal (tiptoeing and releasing silk lines) during the hottest part of the day, under conditions of clear skies and little or no wind (Schneider et al. 2001). The ballooning females mate in their mother colony before dispersal, and after dispersal they establish individual nests that constitute incipient inbred colonies (Henschel 1998; Bilde et al. 2007). We never observed juveniles engaging in aerial dispersal, nor have we ever found new nests established by single juveniles

Figure 1.—Juvenile S. dumicola in tiptoe posture while standing on the underside of a wooden dowel mounted in the wind tunnel. Also visible are a) the dragline leading from the spider's anterior spinnerets to the dowel and b) a partially airborne silk line beginning at the posterior spinnerets and following the air flow upward to the right.
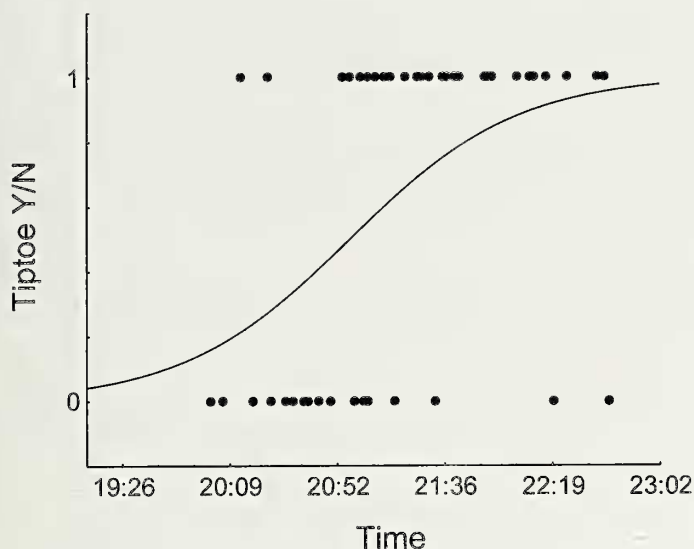
Figure 2.—The probability of tiptoe behavior (yes = 1, no = 0) in juveniles tested at different times of the night. The fitted logistic regression is tiptoe probability = 1/(1+Exp(37.2855-42.6795*x)). Shown here are juveniles collected while engaged in web repair activity (n = 28).

(Schneider et al. 2001; Y. Lubin personal observation). Budding, by contrast, involves movement of a group of large juveniles or subadults a short distance away from the parent nest, and construction of a satellite nest that is initially connected to the parent nest by silk and shares its capture web (Bilde et al. 2007). Budding has not been observed directly, but spiders were seen moving between parent and satellite nests using the connecting web sheets and frame lines (Lubin et al. 2009).

Our observations suggest that tiptoe behavior and release of silk lines by *S. dumicola* juveniles at night are not associated with either ballooning or budding dispersal. First, we observed tiptoeing on the web only at night, and the spiders were all juveniles, thus ruling out ballooning dispersal. Second, spiders that tiptoed on the web released thin lines, but did not become airborne, nor did they turn to grab the lines as in bridging behavior. Third, we found no satellite nests or new groups of juveniles in the vicinity of the study nests during the ten days of observations; thus, budding can be discounted. Finally, in the wind-tunnel experiments, smaller spiders showed a higher frequency of tiptoe behavior; whereas, budding is typically carried out by large juveniles and subadults.

There is some evidence to support the hypothesis that tiptoe behavior in *S. dumicola* is associated with web building. The spiders on the web repeatedly alternated tiptoeing and laying silk on the web; in the wind tunnel, spiders first tiptoed at dusk, coinciding with the start of web building. Finally, there was a non-significant trend of more tiptoeing in spiders collected during web building than during prey capture. We can only speculate about the function of tiptoeing

Table 2.—Body size (prosoma width and total body length, in mm) of juveniles that exhibited tiptoe behavior or did not. Standard deviations are in parentheses. Wald statistie and P values of logistic regression for binomially distributed data; variables were log (x+1) transformed.

Variable	Tiptoe behavior		Wald W, P
	Yes	No	
Prosoma width (n=78)	2.6 (0.31)	2.7 (0.30)	W=4.997, P=0.025
Body length (n=79)	7.1 (0.83)	7.5 (0.91)	W=3.409, P=0.064

and the release of long, thin, free-ended lines in the context of web building. The upward flowing silk lines might snag on branches above the web and could be used later to construct frame lines for new capture web sheets. However, we did not see spiders testing the released lines or climbing up them, which would argue against such a function. Another possibility is that the lines could intercept small, weakly flying insects that would then drop with the silk into the capture sheets below. Free-ended silk lines will move unpredictably with air currents, and flying insects may be unable to avoid them. Producing cribellate capture-web silk is energetically costly both in material and construction time (Lubin 1986; Opell 1998; Pasquet et al. 1999). By contrast, the thin lines are released rapidly and might increase the probability of intercepting insects early in the evening at minimal cost to the spiders. Arguing against this interpretation is the low probability of insects intercepting such lines and their apparent smoothness. Fine cornstarch and talc did not coat the lines (Y. Lubin & R. Suter personal observation), which suggests also that insects might not adhere to them.

Wind-tunnel experiments and the function of tiptoeing.—Spiders in the wind tunnel were in an unfamiliar environment and exposed to continuous, directional wind, conditions that differed from those at the web. Tiptoeing and release of silk usually occurred after a spider ran up and down the dowel one or more times, attached dragline silk, and quested intermittently (see Table 1). Spiders that dropped from the dowel on a dragline sometimes continued to the substrate below. These observations suggest that tiptoeing, dropping on a line and the release of aerial lines in the wind tunnel were escape responses. Thus, "pre-dispersal" behaviors are context-dependent and likely have more than one function in *S. dumicola*: adult, mated females adopt them for aerial dispersal, juveniles release silk while web building for reasons yet to be determined, and stressed or disturbed individuals may use them to escape.

Various wind-tunnel experiments have shown consistent differences among individuals in the frequency of tiptoeing and release of lines in relation to developmental, morphological and life-history traits, as well as different environmental conditions (e.g., inbreeding: Bonte 2009; relative leg length: Corcobado et al. 2012; feeding regime: Bonte et al. 2003; microbial endosymbionts: Goodacre et al. 2009). As in our study, these tests show that some individuals are capable of aerial or bridging movements. Furthermore, some are more likely to do so than others, and this correlates with various traits or conditions. However, although a dispersal function is implied, the contexts in which these "pre-dispersal" behaviors occur under natural conditions should be examined rigorously. In our experiments, we found a size-related difference in tiptoe frequency that is at odds with a dispersal function, but consistent with a web-building function.

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